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Site history affects soil and plant ^{15}N natural abundances ($\delta^{15}N$) in forests of northern Vancouver Island, British Columbia

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Summary

1. About 10 years after establishment, plantations of Western Redcedar (*Thuja plicata* Donn ex D. Don) on northern Vancouver Island, British Columbia become nutrient deficient and chlorotic, grow slowly, and are susceptible to invasion by the ericaceous shrub Salal (*Gaultheria shallon* Pursh.).

2. To test the hypothesis that $\delta^{15}N$ can be related to site histories (site disturbance, soil N dynamics and plant development), we measured soil and foliar $\delta^{15}N$ in the summer of 1992 in 3-year-old (nutrient-sufficient) and 10-year-old (nutrient-deficient) plantations and in old-growth stands. The foliar and soil $\delta^{15}N$ values of the plantations and old-growth forests were different and closely reflected site histories. Salal invasion and nutrient deficiency interacted to depress the growth of Redcedar in 10-year-old plantations.

3. Site preparation destroyed the top soil organic layers (fresh and decaying litter) and forced Salal (ecto- and ericoid mycorrhizal) into the humus layer, where it was in direct competition with Redcedar, thereby disadvantaging arbuscular mycorrhizal/non-mycorrhizal Redcedar in its nutrient acquisition during a period when N and P are severely limited.

4. There was a large seasonal range of foliar $\delta^{15}N$ (5·5 and 4·3‰ for 10-year-old Redcedar and Salal, respectively), and there was no relationship between foliar $\delta^{15}N$ and measured rooting depth, demonstrating that rooting depths cannot be used to explain foliar $\delta^{15}N$ variation among coexisting woody taxa.

5. Foliar and soil $\delta^{15}N$ declined with site age and with a presumed change from 'open' to 'closed' N cycling; the ^{15}N-depleting effects of mycorrhizal N transformations contributed to the observed $\delta^{15}N$ decline.

Key-words: Competition, mycorrhizas, old-growth forest, plantation, slash-burning

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Introduction

While it is self-evident that the $\delta^{15}N$ (the deviation of the naturally occurring ratio of $^{15}N/^{14}N$ of a sample from that of a standard) of any biological sample integrates all of the isotopically fractionating, biogeochemical processes which have contributed to its formation, there is no underpinning mechanism(s) known which adequately explains many patterns of $\delta^{15}N$ found in terrestrial systems (Handley, Scrimgeour & Raven 1998). Hence, the $\delta^{15}N$ values of ecosystem components cannot yet be used as sole indicators of specific processes (Handley & Scrimgeour 1997).

In anticipation of constructing testable models, which may explain such presumably complex suites of mechanisms and allow the use of $\delta^{15}N$ values as indicators of processes, empirical $\delta^{15}N$ patterns of ecosystem samples, site histories, nutrient relations and climate data are required. To this end, $\delta^{15}N$ samples from 3- and 10-year-old plantations and old-growth forests of Western Redcedar (*Thuja plicata* Donn ex D. Don) on northern Vancouver Island, British Columbia were analysed and compared with published information, especially that contained in a more extensive study of soil N dynamics by Chang, Preston & Weetman (1995). In that study, Chang *et al.* showed that: (1) Western Redcedar trees in 10-year-old plantations were chlorotic and grew slowly, symptoms not observed in 3-year-old plantations or in the coexisting shrub Salal (*Gaultheria shallon* Pursh., Ericaceae) on sites

of any age; (2) the 3-year-old plantations had higher foliar N concentrations and lower soil microbial C:N ratios than those of the 10-year-old plantations, and (3) organic layers, rather than mineral soil, are the major nutrient sources for these forest plants (see also Messier & Kimmins 1991). In this paper, we hypothesized that, for sites with different environmental histories, these histories could be related to δ^{15}N for foliage and soils.

Most δ^{15}N studies of terrestrial systems have consisted of pattern identification (Pate, Stewart & Unkovich 1993; Garten & Miegroet 1994; Handley *et al*. 1999). The Vancouver Island forest sites had been studied from a number of perspectives (Prescott & Weetman 1994; Prescott, Weetman & Barker 1996), and we hoped that existing, independent lines of evidence might allow us to interpret δ^{15}N in terms of the nutrient competition between Western Redcedar and Salal in nutrient-deficient 10-year-old plantation stands and to suggest a reason for the observed decline of Western Redcedar vigour in these stands.

Some of the relationships between soil N measurements and foliar δ^{15}N reported here contrast with some published reports for plant–soil systems elsewhere, thus enlarging the variety of reported δ^{15}N patterns.

Materials and methods

STUDY SITES

The study sites (complete details in Chang *et al*. 1995) were on northern Vancouver Island, British Columbia, Canada (50°36′ N, 127°15′ W), in the very wet maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (Pojar, Klinka & Demarchi 1991). Mean annual precipitation at the sites is 1700 mm and mean daily temperatures vary annually from 3·0 °C in January/February to 13·7 °C in July/August (T. Lewis, personal communication).

Three replicates of old-growth stands of Western Redcedar and three replicates each of 3- and 10-year-old Western Redcedar plantations were selected. In the old-growth stands, Western Redcedar reaches diameters at breast height of more than 200 cm, ages of greater than 1000 years, and heights of 40–45 m (Keenan, Prescott & Kimmins 1993); the understorey is dominated by Salal, which grows to > 1 m tall but is not very dense. The cut-overs were slash-burned after logging and then planted with Western Redcedar. The slash-burning had little effect on the humus layer; the organic layers most affected were the fresh litter and decaying litter layers. In the 3-year-old plantations, Salal was dominant (among the understorey plants) but was short (~30 cm) and not very dense. In the 10-year-old plantations, Salal was denser and taller (50–80 cm), and became a strong competitor for the growth-limiting small quantities of soil nutrients (Messier 1993; Chang *et al*. 1996), including N and P (Weetman *et al*. 1989).

Because the sampling sites were selected from similar slope positions and from a relatively small and homogenous area, it is reasonable to assume that the hydrological and pedological processes which affect δ^{15}N variability (e.g. Sutherland *et al*. 1993) were comparable for the plantations and old-growth forests. None of the selected sites had been fertilized.

Timmer & Munson (1991) showed that the N in young trees, derived from high fertilizer applications during container growth, was markedly diluted 1 year after planting out. It is therefore assumed that the trees sampled contained only trivial amounts of the original nursery-applied, fertilizer N. When samples were taken, Western Redcedar trees in the 3-year-old stands were about 30–50 cm tall and those in the 10-year-old stands were > 2 m tall.

The forest-floor organic layer is thick (> 45 cm) and is readily divided into three distinguishable layers: decaying litter (F), woody litter (Fw) and humus (H). In the old-growth forests, the F material consists of partially decomposing fine twigs and leaf litter (~5 cm thick) just below the fresh litter (L) layer. In the 3- and 10-year-old plantations, the F material is only 1–2 cm thick and mainly composed of charred residues. Fw is partially decomposed woody material that retains its structure when rubbed between the fingers. The H material is well decomposed (deMontigny *et al*. 1993) and is the main component of the forest rooting zone (Messier & Kimmins 1991; Chang *et al*. 1995).

FIELD SAMPLING

Current-year foliage samples of Western Redcedar and Salal were taken from all sites on four dates in 1992 (23 May, 16 July, 26 August and 18 October), spanning most of the growing season. On each date, one composite sample of foliage from each plant species was pooled from at least 15 individuals in each stand so that there was one analytical sample from each stand. Western Redcedar foliage was clipped from the upper branches of the 3- and 10-year-old plantations and obtained by shooting off small branchlets of the upper crown with a shotgun in old-growth stands.

On the same four dates, one composite sample of each of the three detritus layers was taken from the forest floor in each stand. Samples were composited from six to seven points within each organic layer within each stand. Although there has been no systematic study of the rooting depths of Redcedar and Salal, field observations made during this study, in a parallel study (Chang *et al*. 1995) and by Cindy Prescott (University of British Columbia, personal communication) have shown that the most likely major sources of nutrients for the two major plant taxa are as given in Table 1. Salal roots spread vegetatively by means of rhizomes and maximal growth is between late April and August (Fraser, Turkington & Chanway 1993). Redcedar forms

Table 1. Organic layers containing the main rooting masses of Western Redcedar and Salal. Parentheses indicate minor sources of nutrients. In young plantation stands, Western Redcedar mainly draws nutrients from the H layer; Salal mainly draws nutrients from the less-decomposed F layer in old-growth stands (Messier & Kimmins 1991)

Stand age	Western Redcedar	Salal
3-year-old	H	H
10-year-old	H	H
Old growth	H (and F)	F (and H)

heart-root systems (Eis 1987) and maximal growth should also occur in the summer.

CHEMICAL ANALYSES

Chemical and isotopic analyses were performed at the Pacific Forestry Centre (Natural Resources Canada, Victoria, B.C.). Foliar samples were analysed for total N content and for $\delta^{15}N$. They were dried at 65 °C overnight and ground to 20-mesh in a Wiley mill (Thomas Scientific, Philadelphia, PA). Total N contents were determined by Kjeldahl digestion followed by steam distillation (Bremner 1965) into boric acid, distilled to about 30 ml. Recovery of N was quantitative. This Winkler modification of the original procedure has the advantage (Bremner 1965) of indicating when distillation is complete, and is useful when dealing with natural abundance level samples, which can be significantly fractionated by incomplete distillation. The NH_3-N collected into boric acid was titrated (using 0·1 M HCl) to determine NH_4^+-N content, dried (at 65 °C) and converted to N_2 via the Rittenberg reaction (Bremner 1965). The dried samples were subjected to a Rittenberg reaction (alkaline sodium hypobromite converts NH_4^+-N to N_2 gas) and the resulting N_2 gas was analysed using a Vacuum Generators Sira 9 isotope-ratio mass spectrometer (VG Isogas, Middlewich, Cheshire, UK) (Chang *et al.* 1996). These manual sample preparations and isotopic analyses were time consuming. However, we were able to analyse ≈ 45% of the samples in duplicate. The precision (standard deviation) of real samples was < 0·3‰, equal to results obtained from modern continuous-flow isotope ratio mass spectrometry (Handley & Scrimgeour 1997).

Delta ^{15}N was expressed in parts per thousand (‰) and calculated as $[(R_{sample}/R_{standard}) - 1] \times 10^3$, where $R = {}^{15}N/{}^{14}N$, and the universally accepted standard is N_2 of air.

All forest floor samples were analysed for microbial biomass N and C (to calculate microbial C:N ratios) and amounts of extractable N; the samples taken on 26 August, only, were additionally analysed for amounts of mineralizable N (Chang *et al.* 1995) and their $\delta^{15}N$ values. Microbial biomass N and C were measured by the chloroform fumigation-extraction method (Brookes *et al.* 1985; Vance, Brookes & Jenkinson 1987). The amounts of mineralizable N (NH_4^+-N released after anaerobic incubation at 30 °C for 2 weeks) were determined by steam distillation and analysed for $\delta^{15}N$ as described for foliar samples. The 26 August samples were used, initially, because soil microbial activity is greatest at this time of year.

Anaerobically mineralizable N has been used widely in forestry and agriculture as a measure of available soil N (Powers 1980; Binkley & Hart 1989). There were also two operational reasons for anaerobic incubation prior to isotopic analyses. First, the fresh samples contained too little NH_4^+-N for direct mass spectrometry on extractable N. Secondly, there are no suitable methods for isolating soil NH_4^+-N for $\delta^{15}N$ analysis (Handley, Scrimgeour & Raven 1998). We therefore sought a standardized, biologically derived N pool against which to judge soil and foliar $\delta^{15}N$. We reasoned that an anaerobic incubation, using the naturally occurring microbial community and performed under standard conditions, would provide a standardized sample of the net amount and $\delta^{15}N$ of freshly mineralized nitrogen, prior to any isotopic changes caused by subsequent transformations.

Results

FOLIAR $\delta^{15}N$

Western Redcedar and Salal (Fig. 1a,b) showed the largest seasonal ranges of foliar $\delta^{15}N$ yet reported (5·5 and 4·3‰ for 10-year-old Redcedar and Salal, respectively), and examination of the curves revealed that 26 August was a suitable sampling date for comparisons of foliar and external $\delta^{15}N$ values (see 'Discussion'). On this date, Western Redcedar foliar $\delta^{15}N$ was ranked as 3-year-old > 10-year-old > old growth; Salal foliar $\delta^{15}N$ was ranked: 3-year-old > old growth > 10-year-old.

SOIL ORGANIC LAYERS

The mineralizable N of soil organic layers (Fig. 1c) became more ^{15}N-enriched with increasing state of decay (which corresponded to increasing depth). The $\delta^{15}N$ of mineralized N from layer F was statistically the same for the two plantations. The $\delta^{15}N$ of mineralized N from the F layer of the old-growth stands was 2·3‰ less than that of the plantations. The Fw (partially decomposed) material showed large variations in N amounts (Chang *et al.* 1995) and $\delta^{15}N$, especially in the 10-year-old and old-growth stands. Mineralized N from the most decomposed layer (H) was greatly ^{15}N-enriched relative to the F layer in stands of all ages, being ranked as 3-year-old > 10-year-old > old growth. This is the same rank order as the foliar $\delta^{15}N$ of Western Redcedar, whose main root mass was in the H layer in stands of all ages, but not the same rank order as the foliar $\delta^{15}N$ of Salal, whose main rooting zone was H in plantations and F in old-growth stands.

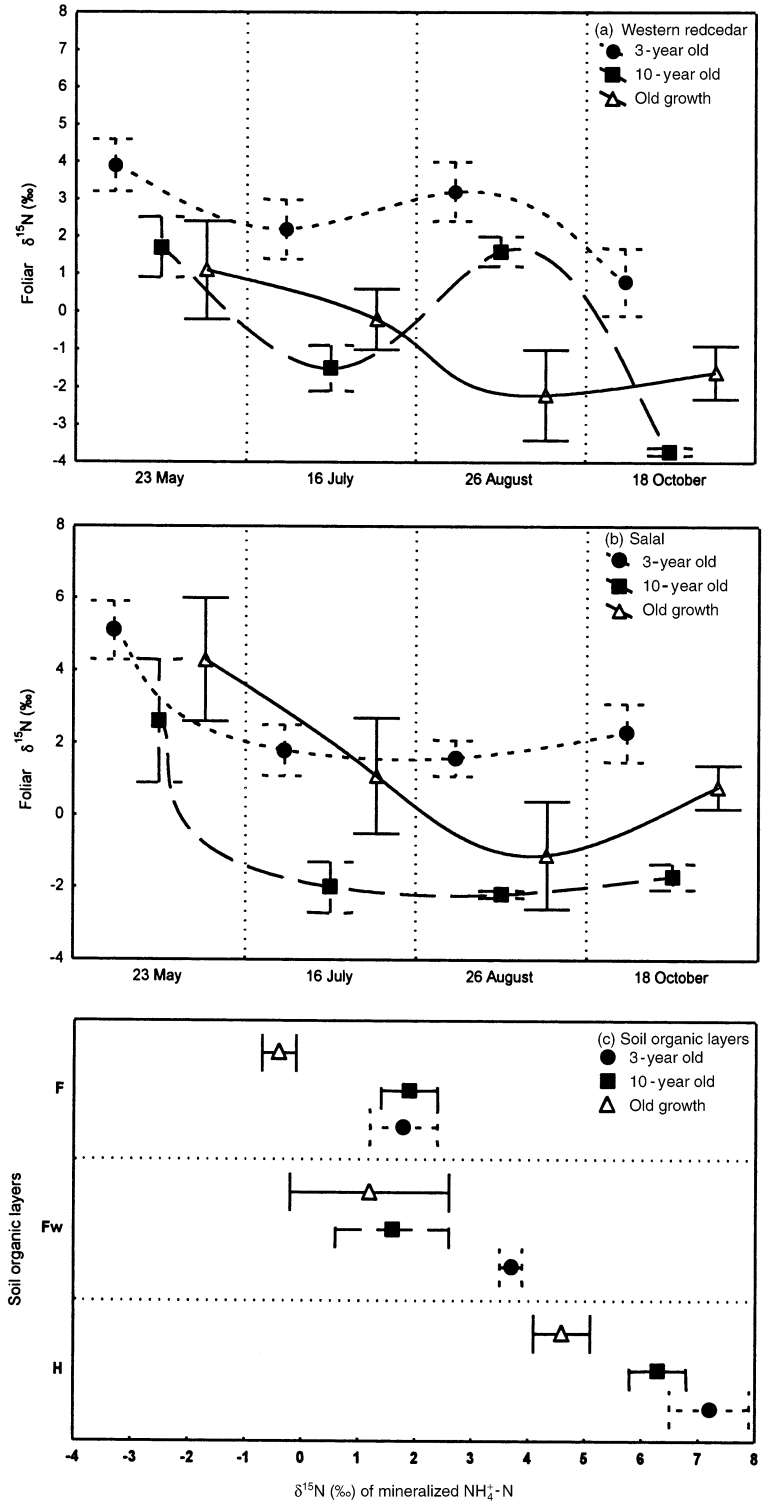

Fig. 1. δ^{15}N of foliage and NH_4^+-N of soil organic layers in 3-year-old, 10-year-old and old-growth stands. (a) Foliar δ^{15}N of Western Redcedar *vs* sampling dates; (b) foliar δ^{15}N of Salal *vs* sampling dates; (c) δ^{15}N of mineralized NH_4^+-N *vs* organic soil layer from which it was derived. Vertical error bars are SEs of means.

Table 2. Simple correlations, for all sites, between foliar ^{15}N data and soil N status as amounts of N and C:N ratios (Chang *et al*. 1995). The Pearson correlation coefficient (r) is given, with significance levels: $*P < 0{\cdot}05$, $**P < 0{\cdot}01$, $***P < 0{\cdot}001$ and NS, non-significant. In the 'Soil variable' column, F, Fw and H refer to forest floor horizons

Soil variable	δ^{15}N Redcedar	δ^{15}N Salal
Ext-N[a], F	NS	NS
Micro-N[b], F	NS	NS
Micro-C:N[c], F	–0·36*	–0·45**
Mineralizable[d] N, F	–0·81**	NS
Ext-N, Fw	NS	NS
Micro-N, Fw	NS	NS
Micro-C:N, Fw	NS	NS
Mineralizable N, Fw	NS	NS
Ext-N, H	NS	NS
Micro-N, H	NS	0·34*
Micro-C:N, H	–0·47**	–0·53**
Mineralizable N, H	–0·78*	NS

[a]Ext-N, total N extracted by 0·5 M K_2SO_4.
[b]Micro-N, microbial biomass N.
[c]Micro-C:N, microbial biomass C:N ratio.
[d]Mineralizable N, NH_4^+-N obtained via anaerobic incubation.

Table 3. δ^{15}N of foliage on 26 August and that of mineralized N from the organic layers sampled on 26 August for three stand ages and the calculated isotopic discriminations between standardized N source (mineralized) and foliage N

	δ^{15}N (‰)			
	Mineralized N[a]		Foliar samples	
Stand age	H	F	Redcedar	Salal
3-year-old	+7·2	–	+3·2	+1·6
10-year-old	+6·3	–	+1·6	–2·2
Old growth	+4·6	–0·4	–2·2	–1·1
			Discrimination[b] (‰)	
3-year-old			–4·0	–5·6
10-year-old			–4·7	–8·5
Old growth			–6·8	–0·7

[a]Standardized N source as mineralizable NH_4^+-N. Layer H contained the main root mass for Redcedar and Salal in the plantations; in old-growth stands, Salal roots were mainly located in the F layer (Table 1).
[b]Discrimination = δ^{15}N of foliage – δ^{15}N of mineralized N.

SOIL VARIABLES *VS* δ^{15}N

The foliar δ^{15}N of Western Redcedar (Table 2) was negatively correlated with the microbial C:N ratio of organic layers F and H, where a larger C:N ratio (e.g. 10-year-old stand, F and H layers) indicated the presence of more fungal biomass (Chang *et al*. 1995), and strongly negatively correlated with the amounts of mineralizable N measured in F and H. The foliar δ^{15}N of Salal was also negatively correlated with measures of microbial C:N, and more strongly than was that of Redcedar. It was also correlated with the amount of microbial N, which that of Redcedar was not. The foliar δ^{15}N of Salal was not correlated with any measures of amounts of mineralizable N.

For the 26 August samples, all foliar $\delta^{15}N$ values (Table 3) were more ^{15}N-depleted than their corresponding standardized N sources. Western Redcedar $\delta^{15}N$ and discriminations, relative to the standardized sources, became steadily more negative with age of stand (Fig. 1a and Table 3). Discrimination for Salal was initially (3-year-old stands) slightly more ^{15}N-depleted than that for Western Redcedar relative to the standardized N sources. In the nutrient-poor 10-year-old stands, Salal discrimination was much more ^{15}N-depleted than that of Western Redcedar; in the old-growth stands, taking into account the difference in the main rooting layers (H *vs* F), the discrimination of Salal relative to the standardized source was statistically nil and the value calculated (–0·7‰) attributable to error.

Discussion

PLANT AND SOIL $\delta^{15}N$

The changes in slope associated with seasonally determined foliar $\delta^{15}N$ have been interpreted as related to major changes in plant N mobilizations (Millard 1996; Handley & Scrimgeour 1997): early spring mobilization of stored N, the increasing effect on foliar $\delta^{15}N$ of externally acquired N, and an autumnal remobilization of N to storage. The foliar $\delta^{15}N$ of Redcedar (Fig. 1a) and Salal (Fig. 1b) exhibited this type of curve; it was therefore possible to infer that the 26 August foliage samples were the most suitable for detailed analysis, because they best reflected the inputs of externally acquired N prior to end-of-season losses.

Western Redcedar $\delta^{15}N$ for 26 August steadily declined from the youngest to the oldest stands (Fig. 1a), as did (Table 3) discrimination against a standard N source. This may primarily have reflected the declining $\delta^{15}N$ of soil mineral N (used by Western Redcedar) with time since site preparation. It also paralleled the age-related discriminations and $\delta^{15}N$ values recorded for layer H (Fig. 1c), i.e. mineralizable N became more ^{15}N-depleted with age of site. Some of the initial decline between 3 and 10 years may be attributable to nutrient stress (Handley *et al.* 1997) and especially to N deprivation (Robinson *et al.* 1999).

Consistent with reports for bulk soil (Martinelli *et al.* 1999) the $\delta^{15}N$ of mineralizable N (Fig. 1c) increased with depth (increasing age and decomposition) of material. Among stand ages, the $\delta^{15}N$ of the mineralizable N from old-growth soils was the most depleted in all layers (Fig. 1c); $\delta^{15}N$ of mineralizable N was greater in the 3-year-old stands than in the 10-year-old stands except in the F layer, where values were equal. The age-related decline of soil and foliar $\delta^{15}N$ supports the conclusions of Handley *et al.* (1999) and Austin & Vitousek (1998) that, as N cycling moves from being relatively 'open' (the 3-year-old plantations) to relatively 'closed' (the old-growth forests) (*sensu* Austin & Vitousek 1998), the $\delta^{15}N$ of major ecosystem components decline. This also implies that lost N becomes increasingly ^{15}N-enriched as it declines in amount, relative to ecosystem N.

Results thus clearly showed that foliar and soil $\delta^{15}N$ values were different between the old-growth forests and plantations and between plantations of different ages. The hypothesis that $\delta^{15}N$ can be related to site histories (site disturbance, soil N dynamics and plant development) is therefore accepted. In the present study it is clear that, in addition to fundamental changes in N cycling, mycorrhizal N transformations played a large part in producing the net change of ecosystem $\delta^{15}N$ (see discussion below).

PLANT MYCORRHIZAL ASSOCIATIONS AND NUTRITION

Foliar $\delta^{15}N$ of Western Redcedar was closely linked with the amount of mineralizable N and only secondarily with microbial biomass C:N ratios in its main rooting zone (H) (Table 2); it was uncorrelated with the amount of microbial N in all layers. Thus our data (Table 2) confirmed and extended existing information on the nutrition of Western Redcedar and were consistent with Western Redcedar largely depending on mineralized N. Western Redcedar is capable of forming arbuscular mycorrhizas but is poorly or not at all mycorrhized when Salal is present (Prescott & Weetman 1994). This being the case, P nutrition would also be impaired under the known P-limitation of 10-year-old stands (Weetman *et al.* 1989).

Redcedar foliar $\delta^{15}N$ was correlated with the same variables in the F layer, where the amount of root biomass was known to be minor. We deem the F-layer correlations to be fortuitous: (1) the F layer is directly formed from plant litter, both from Redcedar and Salal; (2) the $\delta^{15}N$ values of Redcedar and Salal were correlated (+ 0·66), thereby auto-correlating Redcedar $\delta^{15}N$ with all of the litter contributing to the F layer, and (3) dissolved N from the F layer in this acid soil (Chang *et al.* 1995) would percolate into the H layer.

Similarly, for Salal, our data (Table 2) extended existing information (Xiao & Berch 1992; Fraser *et al.* 1993; Prescott & Weetman 1994). Foliar $\delta^{15}N$ of Salal was correlated (Table 2) with the amount of microbial N and highly correlated with microbial biomass C:N ratios in layers F and H. Salal's mycorrhizas allowed it to thrive under nutrient-deficient or nutrient-sufficient conditions, probably accessing all forms of potentially available N. Especially, the changes in Salal foliar $\delta^{15}N$ among sites and the lack of $\delta^{15}N$ correlation with amount of mineral N were consistent with the greatest dependence of foliar $\delta^{15}N$ on mycorrhizas (Hobbie, Macko & Shugart 1999) being in the nutrient-deficient 10-year-old plantations. Salal foliar $\delta^{15}N$ decreased by almost 4‰ (Fig. 1b and Table 3) in the 10-year-old plantations, relative to that in the mineral-nutrient-rich, 3-year-old plantations, and

was intermediate in the old-growth stands where nutrient availability was adequate.

The difference in foliar δ^{15}N between non- or arbuscular mycorrhizal (AM) Western Redcedar and ecto-/ericoid Salal was greatest in nutrient-deficient 10-year-old stands, and the net difference could have resulted from processes increasing the δ^{15}N of Western Redcedar (relative to source N) as well as the lowering of Salal δ^{15}N by mycorrhizal dependence. Azcón, Handley & Scrimgeour (1998) found that the effect of N limitation could raise the δ^{15}N of AM lettuce by as much as 2·5‰; Robinson *et al.* (1999) found a similar effect for N-deficient barley. It has been observed frequently (e.g. Handley *et al*. 1996) that the foliar δ^{15}N of ecto/ericoid mycorrhizal plants is lower than the fungus or bulk soil N. The ability to acquire sufficient N would make Salal a strong competitor for all other nutrients, suggesting that nutrient deficiency played a smaller part in determining Salal foliar δ^{15}N than for Western Redcedar.

ROOTING PATTERN AND INTERSPECIFIC COMPETITION

The F soil layer was largely destroyed by plantation site preparation; neither Western Redcedar nor Salal was rooted substantially in the Fw layer. Hence, site preparation forced Salal and Western Redcedar to compete directly for nutrients in the H layer. Fraser *et al*. (1993) noted that prescribed burning and logging can increase the growth of Salal if the burn is light, as it was in this case.

At the old-growth sites, where there was a well-developed F layer, Salal rooted in this layer and had little direct functional or spatial competition with Redcedar. In the intact and nutrient-rich F layer of old-growth stands, ecto-/ericoid mycorrhizal Salal discriminated slightly relative to standardized, mineralized δ^{15}N and was only about 1‰ different from Western Redcedar. This pattern is consistent with the N-niche concept (Handley & Scrimgeour 1997) and with recent reports of plant δ^{15}N and mycorrhizal symbioses in relation to nutrient availability (Hobbie *et al*. 1999).

It is thus reasonable to suggest that the major detrimental effect of clear-cutting and slash-burning on Western Redcedar plantation growth was caused by placing Redcedar and Salal in direct, spatial and chemical competition for the same limited nutrient supplies. Salal had the competitive advantage in this situation because of its ability to form either ecto- or ericoid mycorrhizas, as required.

NEW δ^{15}N RELATIONSHIPS

Garten & Van Miegroet (1994) found that rates of mineralization in a nitrifying soil were positively correlated with the foliar δ^{15}N of some woody taxa. In the present study, where NH_4^+-N was the major form of extractable mineral N, foliar δ^{15}N was negatively correlated with amount of mineralizable N.

Pate *et al*. (1993) found in semiarid Western Australia that the effects of burning on foliar δ^{15}N disappeared within 5 years; Schulze *et al*. (1998) could find no effects of burning on foliar δ^{15}N on the Northern Australian Transect. In the present work, the indirect effects of fire on foliar δ^{15}N were large after 10 years.

Variations in rooting depths have been used to explain variations in foliar δ^{15}N among woody taxa sharing a site (e.g. Schulze, Chapin & Gebauer 1994). This explanation was based on the reasoning that foliar δ^{15}N would mirror the frequently observed increase of bulk soil δ^{15}N with depth in old, stable forest soils. Our data do not support this explanation for differences of foliar δ^{15}N among plant taxa. Where main rooting depths were different, the δ^{15}N relationships were not as predicted by this reasoning; where main rooting depths were the same, foliar δ^{15}N values were substantially different between species.

The range of seasonal foliar δ^{15}N variation appears to differ among different types of site. Handley & Scrimgeour (1997) found significant variation in north maritime coastal scrub, averaging about 1·5 to 3‰ for different taxa. Kielland, Barnett & Schell (1998) found little seasonal variation (about 0·7 to 1·5‰) for the foliar δ^{15}N of six woody taxa in Alaska. In the present work, seasonal variation was large (up to 5·5‰ for Redcedar and 4·3‰ for Salal at nutrient-deficient sites).

Conclusions

Our data show that recent site histories of these northern forests are reflected in foliar and soil δ^{15}N and that, given independent lines of evidence, δ^{15}N values can assist in suggesting mechanisms underpinning observed plant behaviours. We conclude that plantation site preparation, which includes slash-burning, forces Salal out of its normal N-niche in the relatively undecomposed F layer and into direct competition with Western Redcedar in the H layer, thereby disadvantaging Western Redcedar in nutrient acquisition under nutrient-limited conditions. This occurs because Salal is able to access all of the major chemical forms of available N via its ericoid- and ecto-mycorrhizal habit, while Western Redcedar must chiefly depend on mineralized N. Mycorrhizal N transformations contributed to the previously observed relationships between the δ^{15}N of major ecosystem components and their presumed 'openness' of N cycling. We found that seasonal changes of foliar δ^{15}N were large, and rooting depth was not related to foliar δ^{15}N variations at sites of any age.

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References

Austin, A.T. & Vitousek, P.M. (1998) Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia* **113**, 519–529.

Azcón, R., Handley, L.L. & Scrimgeour, C.M. (1998) The $\delta^{15}N$ of lettuce and barley are affected by arbuscular mycorrhizal status and by external concentrations of N and P. *New Phytologist* **138**, 19–26.

Binkley, D. & Hart, S. (1989) Components of nitrogen availability assessments in forest soils. *Advances in Soil Science* **10**, 57–116.

Bremner, J.M. (1965) Total nitrogen: section 83. *Methods of Soil Analysis: Chemical and Microbiological Properties* (eds C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger & F. E. Clark), pp. 1149–1178. American Society of Agronomy, Madison, WI.

Brookes, P.C., Kragt, J.F., Powlson, D.S. & Jenkinson, D.S. (1985) Chloroform fumigation and the release of soil nitrogen: the effects of fumigation time and temperature. *Soil Biology and Biochemistry* **17**, 831–835.

Chang, S.X., Preston, C.M. & Weetman, G.F. (1995) Soil microbial biomass and microbial and mineralizable N in a clear-cut chronosequence on northern Vancouver Island, British Columbia. *Canadian Journal of Forest Research* **25**, 1595–1607.

Chang, S.X., Preston, C.M., McCullough, K., Weetman, G.F. & Barker, J. (1996) Understory competition effect on distribution and recovery of ^{15}N on a western redcedar–western hemlock cut-over site on northern Vancouver Island. *Canadian Journal of Forest Research* **26**, 313–321.

deMontigny, L.E., Preston, C.M., Hatcher, P.G. & Kogel-Knaber, I. (1993) Comparison of humus horizons from two ecosystem phases on northern Vancouver Island using ^{13}C NMR spectroscopy and CuO oxidation. *Canadian Journal of Soil Science* **73**, 9–25.

Eis, S. (1987) Root systems of older immature hemlock, cedar, and Douglas-fir. *Canadian Journal of Forest Research* **17**, 1348–1354.

Fraser, L., Turkington, R. & Chanway, C.P. (1993) The biology of Canadian weeds. 102. *Gaultheria shallon* Pursh. *Canadian Journal of Plant Science* **73**, 1233–1247.

Garten, C.T. Jr & van Miegroet, H. (1994) Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. *Canadian Journal of Forest Research* **24**, 1636–1645.

Handley, L.L. & Scrimgeour, C.M. (1997) Terrestrial plant ecology and ^{15}N natural abundance: the present limits to interpretation for uncultivated systems with original data from a Scottish old field. *Advances in Ecological Research* **27**, 133–212.

Handley, L.L., Brendel, O., Scrimgeour, C.M., Schmidt, S., Raven, J.A., Turnbull, M.H. & Stewart, G.R. (1996) The ^{15}N natural abundance patterns of field-collected fungi from three kinds of ecosystems. *Rapid Communications in Mass Spectrometry* **10**, 974–978.

Handley, L.L., Robinson, D., Forster, B.P., Ellis, R.P., Scrimgeour, C.M., Gordon, D.C., Nsnmevo, E. & Raven, J.A. (1997) Shoot $\delta^{15}N$ correlates with genotype and salt stress in barley. *Planta* **102**, 100–102.

Handley, L.L., Scrimgeour, C.M. & Raven, J.A. (1998) ^{15}N natural abundance levels in terrestrial vascular plants: a précis. *Stable Isotopes: Integration of Biological, Ecological and Geochemical Processes* (ed. H. Griffiths), pp. 89–98. BIOS Scientific Publishers, Oxford.

Handley, L.L., Austin, A.T., Robinson, D., Scrimgeour, C.M., Raven, J.A., Heaton, T.H.E., Schmidt, S. & Stewart, G.R. (1999) The 15-N natural abundance ($\delta^{15}N$) of ecosystem samples reflects measures of water availability. *Australian Journal of Plant Physiology* **26**, 185–199.

Hobbie, E.A., Macko, S.A. & Shugart, H.H. (1999) Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprophytic fungi from isotopic evidence. *Oecologia* **118**, 353–360.

Keenan, R.J., Prescott, C.E. & Kimmins, J.P. (1993) Mass and nutrient content of woody debris and forest floor in western redcedar and western hemlock forests on northern Vancouver Island. *Canadian Journal of Forest Research* **23**, 1052–1059.

Kielland, K., Barnett, B. & Schell, D. (1998) Intraseasonal variation in the $\delta^{15}N$ signature of taiga trees and shrubs. *Canadian Journal of Forest Research* **28**, 485–488.

Martinelli, L.A., Piccolo, M.C., Townsend, A.R., Vitousek, P.M., Cuevas, E., McDowell, W., Robertson, G.P., Santos, O.C. & Treseder, K. (1999) Nitrogen stable isotopic composition of leaves and soil: tropical *versus* temperate forests. *Biogeochemistry* **46**, 45–65.

Messier, C. (1993) Factors limiting early growth of western red cedar, western hemlock and Sitka spruce seedlings on ericaceous-dominated clearcut sites in coastal British Columbia. *Forest Ecology and Management* **60**, 181–206.

Messier, C. & Kimmins, J.P. (1991) Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria Shallon* in coastal British Columbia. *Forest Ecology and Management* **46**, 275–294.

Millard, P. (1996) Ecophysiology of the internal cycling of nitrogen for tree growth. *Zeitschrift für Pflanzenernährung und Bodenkunde* **159**, 1–10.

Pate, J.S., Stewart, G.R. & Unkovich, M. (1993) ^{15}N natural abundance of plant and soil components of a *Banksia* woodland ecosystem in relation to nitrate utilisation, life form, mycorrhizal status and N_2-fixing abilities of component species. *Plant, Cell & Environment* **16**, 365–373.

Pojar, J., Klinka, K. & Demarchi, D.A. (1991) Coastal western hemlock zone. *Ecosystems of British Columbia* (eds D. Meidinger & J. Pojar), pp. 95–111. British Columbia Ministry of Forests, Victoria, B.C.

Powers, R.F. (1980) Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. *Soil Science Society of American Journal* **44**, 1314–1320.

Prescott, C.E. & Weetman, G.F. (1994) *Salal Cedar Hemlock Integrated Research Program: A Synthesis*. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Prescott, C.E., Weetman, G.F. & Barker, J.E. (1996) Causes and amelioration of nutrient deficiencies in cutovers of cedar-hemlock forests in coastal British Columbia. *Forestry Chronicle* **72**, 293–302.

Robinson, D., Handley, L.L., Scrimgeour, C.M., Ellis, R.P., Forster, B.P., Gordon, D.C. & Keith, R. (2000) Using

stable isotope natural abundances (δ^{15}N and δ^{13}C) to integrate the stress responses of wild barley (*Hordeum spontaneum* C. Koch.) genotypes. *Journal of Experimental Botany* **51**, 9–17.

Schulze, E.-D., Chapin, F.S. III & Gebauer, G. (1994) Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia* **100**, 406–412.

Schulze, E.-D., Williams, R.J., Farquhar, G.D., Schulze, W., Langridge, J., Miller, J.M. & Walker, B.H. (1998) Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* **25**, 413–425.

Sutherland, R.A., van Kessel, C., Farrell, R.E. & Pennock, D.J. (1993) Landscape-scale variations in plant and soil nitrogen-15 natural abundance. *Soil Science Society of America Journal* **57**, 169–178.

Timmer, V.R. & Munson, A.D. (1991) Site-specific growth and nutrition of planted *Picea mariana* in the Ontario Clay Belt. IV. Nitrogen loading response. *Canadian Journal of Forest Research* **21**, 1058–1065.

Vance, E.D., Brookes, P.C. & Jenkinson, D.S. (1987) An extraction method for measuring soil microbial biomass C. *Soil Biology & Biochemistry* **19**, 703–707.

Weetman, G.F., Fournier, R., Barker, J. & Schnorbus-Panozzo, E. (1989) Foliar analysis and response of fertilized chlorotic western hemlock and western redcedar reproduction on salal-dominated redcedar-hemlock cutovers on Vancouver Island. *Canadian Journal of Forest Research* **19**, 1512–1520.

Xiao, G. & Berch, S.M. (1992) Ericoid mycorrhizal fungi of *Gaultheria shallon*. *Mycologia* **84**, 470–471.

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